

CHROMOSOMAL INVERSIONS IN *DROSOPHILA ALBOMICANS* IN TAIWAN¹

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Fei-Jann Lin and Hwei-Yu Chang (1986) Chromosomal inversions in *Drosophila albomicans* in Taiwan. *Bull. Inst. Zool., Academia Sinica* 25(2): 129-134. Salivary gland chromosomes of *Drosophila albomicans* collected from 13 localities in Taiwan were analysed for chromosomal inversions. Eight heterozygous inversions have been detected, 1 on X-chromosome, 2 on 2R-chromosome, 1 on 2L-chromosome, and 4 on 3-chromosome. The dot-shaped 4-chromosome is so short that no inversion has ever been found in this laboratory. Since Kending has the most polymorphic population among these 13 localities, it might be the distribution origin of *Drosophila albomicans* in Taiwan. In addition, the distribution of *Drosophila albomicans* is split by the Central Mountain Range. In the east, the patterns of inversion are more complicated than those in the west.

Key words: *Drosophila, inversion polymorphism.*

Chromosomal polymorphisms in natural populations over thirty species of *Drosophila* have been studied (Carson *et al.*, 1970; Dobzhansky, 1970; Ferrari and Taylor, 1981; Fontdevila 1982; Krimbas and Loukas, 1980; Prevosti, 1974; Wasserman, 1982; Wright, 1978). Those studies have thrown some light upon the evolutionary processes as well as the genetic systems of the super-genes and of the heterozygous advantages in maintaining and controlling polymorphisms in natural *Drosophila* populations. As reported by Dobzhansky (1970), the amount of chromosomal polymorphisms is related to the diversity of ecological niches occupied by the populations. In fact, a population in the center of its distributional range occupies a great number of different ecological niches and shows highly polymorphic in chromosomal inversions (Carson, 1959, 1965; Carson and Heed,

1964). Thus, the investigation of inversion polymorphism will provide valuable information to understand the origin of distribution and the historical processes of diversification.

Since we have established the standard map of the giant chromosomes of *Drosophila albomicans* (Lin, *et al.*, 1974), the purposes of this communication are (1) to reveal the geographical patterns of the distribution of inversions in *D. albomicans* in Taiwan, and (2) to investigate the origin of distribution and the historical processes of diversification within species of *D. albomicans* in Taiwan.

MATERIALS AND METHODS

Drosophila albomicans were collected from Nangang (Ng, 南港), Taipei City; Wulai (Wl, 烏來), Taipei County; Jiuntou (Jt, 墳頭), Yilan County; Shrtoushan (Ss, 獅頭山), Shinju County; Puli (Pl, 埔里), Nantou

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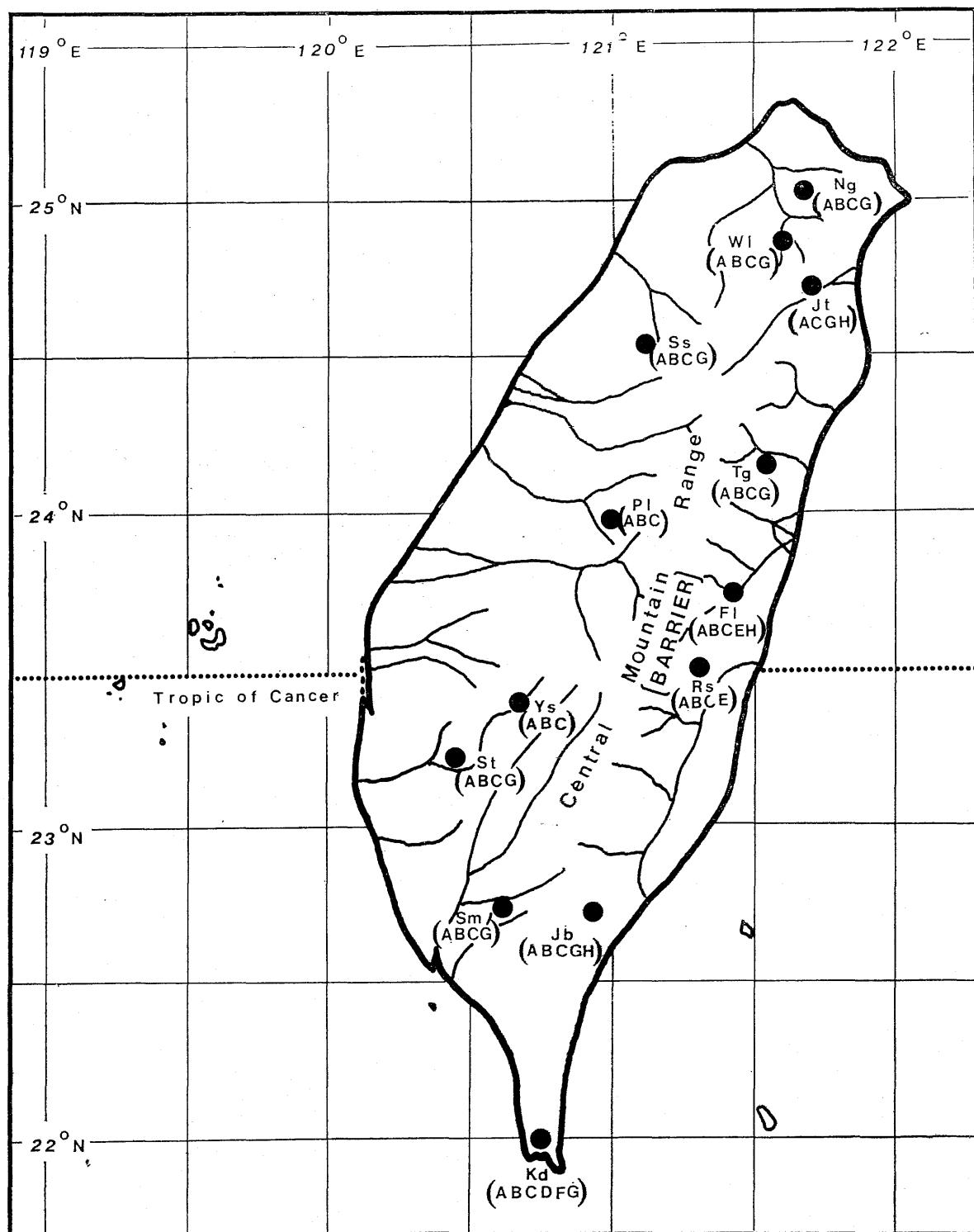


Fig. 1. Thirteen collecting sites of *Drosophila albomicans* are indicated on the map of Taiwan. Types of inversions are enclosed in parentheses.

County; Yuenshuei (Ys, 泰水), Jia-yi County; Shanhutan (St, 珊瑚潭), Tainan County; Juben (Jb, 知本), Taidung County; Sandimen (Sm, 三地門), and Kending (Kd, 墾丁), Ping-dung County; and Tailuge (Tg, 太魯閣), Funglin (Fl, 凤林), and Rueisuei (Rs, 瑞穗), Hwalian County (Fig. 1). Isofemale lines were established after the collection. All strains were reared in the laboratory condition with 22°C and 75% relative humidity throughout the experiment. Third instar female larvae were dissected in 45% acetic acid quickly. The salivary glands were exposed to the acid for one minute and then submerged in 1 N HCl for 15 to 30 seconds. After the glands were stained in lacto-aceto-orcein for 20 minutes, they were squashed on a slide in 75% lacto-acetic acid (1: 1.5) under the thumb pressure on a cover slip. The slides were then examined under a microscope and inversion types were identified according to the standard map of the giant chromosomes (Lin, *et al.* 1974). The heterozygosity of each inversion type in different localities was calculated by a formula: number of individuals with heterozy-

gous inversion/total number of individuals examined.

RESULTS

The number of isofemale stocks established from 13 localities in this island are shown in Table 1. Totally, 3,513 individual female larvae from 80 isofemale stocks were dissected and their salivary gland chromosomes were examined for the heterozygous inversions. Eight heterozygous inversion types, named Type A through H, were observed: In (1)A₁A₄, In(2L)A₂B₄, In(2L)B₁D₅, In(2R)A₁A₅, In (3)A₁A₄, In(3)A₁B₁, In(3)A₁B₄, In(3)M₅O₄ (Table 1). No inversion in 4-chromosome has been observed. The frequencies of heterozygous inversion types range from 0.002 to 0.201. The heterozygous inversion In(2L)B₁D₅ is the most prominent type in *D. albomicans* in Taiwan.

The distribution of inversion types in different localities are shown in Fig. 1. The flies at Kending have six out of eight inversion types, hence the population there seems to be the most polymorphic one in Taiwan.

TABLE 1
Chromosomal inversion types and their frequencies in *Drosophila albomicans* populations in Taiwan

Localities	Isofemale stocks	Number of Individuals	Heterozygosity of Various Inversion Types*							
			A	B	C	D	E	F	G	H
Ng	6	225	.033	.008	.077	0	0	0	.013	0
W1	13	444	.020	.004	.103	0	0	0	.007	0
Jt	4	185	.021	0	.070	0	0	0	.007	.019
Ss	4	158	.036	.006	.041	0	0	0	.030	0
Tg	5	246	.021	.004	.151	0	0	0	.010	0
P1	6	300	.019	.010	.119	0	0	0	0	0
Ys	10	448	.025	.009	.028	0	0	0	0	0
St	5	243	.019	.006	.103	0	0	0	.006	0
Jb	6	273	.024	.010	.145	0	0	0	.009	.005
Sm	4	177	.024	.006	.201	0	0	0	.008	0
Kd	8	377	.031	.010	.126	.002	0	.004	.014	0
Fl	5	250	.028	.017	.075	0	.014	0	0	.006
Rs	4	187	.021	.010	.054	0	.008	0	0	0

* Type A=In(1)A₁A₄; Type B=In(2L)A₂B₄; Type C=In(2L)B₁D₅; Type D=In(2R)A₁A₅; Type E=In(3)A₁A₄; Type F=In(3)A₁B₁; Type G=In(3)A₁B₄; Type H=In(3)M₅O₄

No cline of frequencies of any inverison type has been found across the distribution area. Two of the inversions, In(1)A₁A₄ and In(2L)B₁D₅, occur over the entire distribution area, but no population has the complete collection of inversions found. As shown in Fig. 1, the Central Mountain Range seems to be a natural geographic barrier for the distribution of *D. albomicans* in Taiwan. The distribution of inversion types in the western part of this island is more uniform than that in the eastern part. In general, there are two sets of inversion found in the west. Flies collected from Puli and Yuenshuei near Central Mountain Range have three inversion types including In(1)A₁A₄, In(2L)A₂B₄ and In(2L)B₁D₅. In the remaining 5 localities in the west, one more inversion, In(3)A₁B₄, is observed. However, the inversion patterns get more complicated in the eastern part of Taiwan. Each locality contains a different collection of heterozygous inversions in the east.

DISCUSSION

Inversion polymorphisms are different from isozyme polymorphisms in several ways. One of which is that inversions appear to be high polymorphic in central and low polymorphic in peripheral populations. According to the view of selectionist, peripheral populations are often small, have less available niches to occupy, and are dominated by "homoselection" (Carson, 1959; Dobzhansky, 1970). In addition, because of the extremely low mutation rate of non-deleterious inversions, the number of inversion types maintained in a population can also be influenced by drift and migration. Thus, the inversion data not only indicate the distribution center but also reflect the size and the degree of insulation of populations.

Since Kending has the most polymorphic population among the thirteen localities, we suggest that Kending may be the distribution center on this island. According to the report of Kitagawa, *et al.* (1982), the distribu-

tion of *D. albomicans* is from India through Thailand, Taiwan and then to several Japanese islands of the Ryukyu Group, i.e., from south to north. Therefore, it is not surprised that Kending, which is southernmost on this island, is the distribution center of *D. albomicans*.

After colonization at Kending, *D. albomicans* expanded the distribution range from south to north all over the island under an altitude of 1,500 meter. The distribution has been split by the Central Mountain Range with the average altitude of more than 3,000 meter. Among western populations, *D. albomicans* at Yuenshei and Puli have the least number of inversion types. These results seem to be consistent to Carson's hypothesis (Carson, *et al.*, 1970), because these two localities are near Central Mountain Range and hence are more isolated or smaller than the rest. The degree of insulation seems to be higher among eastern populations because each population has its unique combination of inversion types. It is probably due to the complicated topography. Furthermore, the presence of most of the inverison types at Kending may indicate that a big population has been maintained there.

The heterozygous inversion 2LB₁D₅ is present in all the populations, and has an average frequency of 0.10. In fact, a high heterozygosity of inversion 2LB₁D₅ has also been observed in natural population at Wulai (unpublished data). Therefore, this heterozygous inversion type may contribute certain selective advantage.

Without considering transposable elements, there is little possibility for a specific chromosomal inversion to occur twice. In other words, a particular inversion type will only occur once, at a single locality (White, 1978). Since they have single origin, they are ideal tools for the study of evolutionary history. Phylogenetic chart of the gene arrangements can be constructed with the aid of the theory of overlapping inversions (Dobzhansky, 1970). However, have no overlapping

inversions been found in this study, hence the relationships among the inversions reported here can not be determined by this theory.

Furthermore, it is not a suitable way of using those data to construct the phenogram, because (1) the effective nondeleterious mutation rate is too low that the absence of a particular inversion in two populations might be due to drift instead of similarity or phylogenetic closeness; (2) the number of inversion types is not big enough for numerical methods; and (3) all of those inversions are floating instead of being fixed in populations.

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REFERENCES

CARSON, H. L. (1959) Genetic conditions which promote or retard the formation of species. *Cold Spring Harbor Symp. Quant. Biol.* 24: 87-105.

CARSON, H. L. (1965) Chromosomal polymorphism in geographically widespread species of *Drosophila*. In *The Genetics of Colonizing Species* (H. G. Baker and G. L. Stebbins, eds.). Academic Press, New York pp. 508-531.

CARSON, H. L. and W. B. HEED (1964) Structural homozygosity in marginal populations of nearctic and neotropical species of *Drosophila* in Florida. *Proc. Natl. Acad. Sci.* 52: 427-430.

CARSON, H. L., D. E. HARDY, H. T. SPIETH and W. S. STONE (1970) The evolutionary biology of the Hawaiian Drosophilidae. In *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky* (M. K. Hecht and W. C. Steere, eds.). Appleton-Century-Crofts, New York. pp. 437-543.

DOBZHANSKY, Th. (1970) *Genetics of the Evolutionary Process* Columbia Univ. Press, New York. 505 pp.

FERRARI, J. A. and C. E. TAYLOR (1981) Hierarchical patterns of chromosome variation in *Drosophila subobscura*. *Evolution* 35: 391-394.

FONTEDEVILA, A. (1982) Recent developments on evolutionary history of the *Drosophila mulleri* complex in South America. In *Ecological Genetics and Evolution* (J. S. F. Barker and W. T. Starmer, eds.). Academic Press Inc., New York. pp. 81-95.

KITAGAWA, O., K-I. WAKAHAMA, Y. FUJAMA, Y. SHIMADA, E. TAKANASHI, M. HATSUMI, M. UWABO and Y. MITA (1982) Genetic studies of the *Drosophila nasuta* subgroup, with notes on distribution and morphology. *Jpn. J. Genet.* 57: 113-141.

KRIMBAS, C. and M. LOUKAS (1980) The inversion polymorphism of *Drosophila subobscura*. *Evol. Biol.* 12: 163-234.

LIN, F. J., H. C. TSENG and T. C. WANG (1974) Standard map of the salivary gland chromosomes of *Drosophila albomicans* Duda. *Dros. Inf. Serv.* 51: 42-43.

PREVOSTI, A. (1974) Chromosomal inversion polymorphism in the southwestern range of the *Drosophila subobscura* distribution area. *Genetica* 45: 111-124.

WASSERMAN, M. (1982) Cytological evolution in the *Drosophila repleta* species group. In *Ecological Genetics and Evolution* (J. S. F. Barker and W. T. Starmer eds.) Academic Press Inc., New York. pp. 49-64.

WHITE, M. J. D. (1978) *Modes of Speciation* Freeman and Co., San Francisco. 455 pp.

WRIGHT, S. (1978) *Genetics and the evolution of populations. IV. Variability within and among natural populations*. Univ. Chicago Press, Chicago. 474 pp.

臺灣地區紅果蠅 (*Drosophila albomicans*) 之染色體逆位

林 飛 機 張 慧 羽

由本省十三個地點採集的紅果蠅之唾液腺染色體逆位分析，發現八個異結合型逆位；X染色體、第二對染色體右臂、左臂與第三對染色體分別有1, 2, 1及4個。點狀的第四對染色體非常短，並未發現異結合型逆位。在這十三個地點中，以墾丁的紅果蠅多態性最强，它可能是紅果蠅在本省分佈的起源，而且可能一直維持着相當大的族羣。調查結果亦顯示紅果蠅的分佈受中央山脈的分隔；逆位的型式以東部較複雜。